

RESOURCE OVERLAP BETWEEN MOUNTAIN GOATS AND BIGHORN SHEEP

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ABSTRACT.—Mountain goat (*Oreamnos americanus*) and bighorn sheep (*Ovis canadensis*) ranges overlap substantially in northwestern United States and southwestern Canada. Resource overlap in food and habitat parameters is assumed, but the degree of overlap has not been estimated. Data from published separate and comparative studies on food and habitat use were used to calculate indices of resource overlap for goats and sheep. Indices of overlap for general forage classes (grasses, forbs, browse) were >0.90 in summer and winter for data based on pooled data from separate studies and in summer for data from comparative studies. In winter for comparative studies this overlap was 0.64. For studies where forage species were identified, estimates of resource overlap from separate studies were ~ 0.8 but were <0.5 for comparative studies. Indices of overlap for habitat variables were also low (<0.7) for comparative studies. It was concluded that possible overlap in food and habitat use by goats and sheep could be extensive; but in sympatric populations, resource overlap may be reduced substantially.

Key words: bighorn sheep, mountain goats, *Oreamnos americanus*, *Ovis canadensis*, resource overlap, resource partitioning.

In the northwestern United States, Rocky Mountain goats (*Oreamnos americanus*) historically ranged south along the Bitterroot Divide to near the Continental Divide between Idaho and Montana and in the Cascade Mountains south to central Washington (Hall 1981). With the gradual extension of European settlement, goats were extirpated from numerous areas. Beginning in the early 1900s, goats were transplanted into their historic range as well as other suitable habitats, e.g., Colorado, northwest Washington. Many of these areas where goats were not recently found were historic ranges of bighorn sheep (*Ovis canadensis*). The introduction of mountain goats into the range of bighorn sheep raised concerns regarding potential impacts of goats on bighorns. Because goats and sheep are generalist herbivores that use subalpine to alpine environments, it is commonly assumed their food and habitat requirements overlap extensively in these areas. Based on this assumption, some researchers have expressed concern that goats might compete with sheep when introduced into existing sheep range. Although the outcome of this competition is uncertain, goats are thought to be the superior competitors (Whitfield 1983). Concern about potential competition has caused a reevalua-

tion of introducing goats into areas beyond their historic range, especially in areas containing bighorn sheep. However, resource overlap, which must not be confused with competition, does not justify sweeping generalizations about competitive interactions. Additionally, the assumption of extensive resource overlap is based primarily on food and habitat use by goats and sheep from studies separated by space and time. It is unclear whether data from such diverse studies can be used to infer resource overlap of these two species in sympatry. Consequently, the implication of competition between goats and sheep is tenuous and should not be used to influence reintroduction decisions without a review and reassessment of resource overlap between these two species.

There are many studies on food habits and habitat use of goats and sheep. However, most are unpublished theses. There has yet to be a comprehensive review of existing literature, nor have any estimates of resource overlap been reported. My objectives were to (1) review and summarize available literature on food and habitat utilization of Rocky Mountain goats and bighorn sheep and (2) reevaluate and quantify, if possible, the amount of resource overlap that exists between these

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two species. Only with such a review and reevaluation can we proceed to set up rigid experimental designs to address questions concerning potential competition between goats and sheep.

METHODS

I compiled data from 34 separate studies on food habits and habitat use of sheep and goats and from 3 comparative studies of sympatric populations. Some separate studies were of known allopatric populations because the study areas were outside the range of the corresponding sheep or goat species. Most studies were in areas where both species occurred, but the reports did not indicate whether the corresponding species was in the study area. Because I could not assume allopatry in all studies, this term is not used in reference to these separate studies.

Methods of data collection varied among studies. Most authors expressed food habits as percentage of observed use or occurrence in stomach or feces but did not adjust their estimates for forage availability (Rominger and Bailey 1982). Some researchers classified forage only by classes (grass, forbs, or shrubs); others presented lists of forage species. Most researchers quantified diets separately for either summer or winter or both. A few researchers presented diets for spring and fall, but there were insufficient data to include these seasons in this analysis.

I expressed food habits data as percentage of use by category. I used these data to calculate resource overlap indices (O) based on equation 1 (Lawlor 1980):

$$o_{jk} = \sum p_{ij} p_{kj} [\sum (p_{ij})^2 * \sum (p_{kj})^2]^{1/2} \quad [1]$$

Where: p_{ij} and p_{kj} are the proportions of resource type j used by species i and k .

The index O ranges from 0 (no overlap) to 1.0 (total overlap). Indices of overlap were calculated for all combinations of food categories (forage classes, species), season (winter, summer), and study status (separate, comparative) except specific winter diets from comparative studies for which no data were available. Pooled data from separate studies were used to calculate one set of resource overlap indices; data from comparative studies were

used to determine additional indices for each study. Calculations of resource overlap for forage species from separate studies were limited to studies from subalpine and alpine areas in the northwestern U.S. where sheep and goats co-occur. Food habits reflect availability of food species (Rominger and Bailey 1982), which in more northern areas for goats and more southern areas or lower elevations for sheep can differ greatly, biasing any comparisons that might be made. Restricting this review to data from subalpine and alpine areas in the northwest region should limit differences in resource availability to an acceptable level.

Several investigators reported percentage of habitat utilized by goats and sheep. Comparing data from these studies was difficult because habitat classifications were not standardized. In these studies general patterns of habitat use were summarized. For the few comparative studies of sympatric populations, habitat overlap indices were calculated with equation 1. In separate studies some authors measured physical characteristics of the environment selected by animals, specifically, distance to escape cover, elevation, and slope. Data were not expressed in percent use of different categories but were means of observations. These data were compared with t test or analysis of variance designs as appropriate. The null hypothesis was no difference in means for goats and sheep for the tested characteristic. Acceptance of the null hypothesis would indicate total resource overlap. Rejection ($P < .05$) of the null indicates significant statistical separation along the tested resource axis.

RESULTS

Food Habits

Several investigators presented only qualitative assessments of goat and sheep diets (Davis 1938, Honess and Frost 1942, Spencer 1943, Casebeer 1948, Couey 1950, Smith 1954, McCann 1956, Berwick 1968, Cooper-rider 1969). Diets were similar in summer and winter, with both species relying on grasses and forbs. Where authors estimated diet compositions, data indicated that goats relied on grasses (52%) and forbs (30%) in summer but shifted to grasses (60%) and shrubs (32%) in winter (Table 1). Sheep (Table 1) used mainly

TABLE 1. Summary of general forage classes used by goats and sheep from various studies in alpine and subalpine habitats. Estimates are expressed as percent of total use and are based on either fecal or rumen analyses. Locations of studies are indicated by standard U.S. Postal Service codes.

Species Reference	Summer			Winter		
	Grass	Forb	Browse	Grass	Forb	Browse
MOUNTAIN GOATS						
Saunders 1955 MT	76	14	2	59	10	30
Hilbs 1967 CO	97	3	0	88	0	12
Peck 1972 MT	22	78	0	90	6	1
Pallister 1974 MT	40	60	0			
Johnson et al. 1978 CO	60	29	7			
Thompson 1981 CO	84	15	1			
Thompson 1981 MT	11	9	79	47	2	51
Stewart 1975 MT	47	53	0			
Johnson 1983 WA	44	20	35	31	3	65
Campbell & Johnson 1983 WA	43	20	36			
Adams & Bailey 1983 CO				45	24	30
\bar{x}	52	30	16	60	8	32
BIGHORN SHEEP						
Mills 1937 WY	60	35	5	98	0	0
Moser 1962 CO	75	6	19			
Pallister 1974 MT	12	55	32	98	2	0
Frisina 1974 MT	95	4	1	92	6	1
Stewart 1975 MT	44	47	8	40	40	20
Todd 1975 CO	65	6	29	23	11	67
Johnson & Smith 1980 NM	46	50	4	83	10	7
Whitfield 1983 WY	25	12	63	30	32	39
Martin 1985 MT	74	16	10	39	50	10
Estes 1979 WA	30	8	62	62	3	35
Honess & Frost 1942 WY	51	30	19			
Harrington 1978 CO	88	12	0			
Kasworm et al. 1984 MT				65	12	23
Blood 1967 BC				54	5	40
Constan 1972 MT				72	17	8
Keating et al. 1985 WY				56	7	38
Schallenberger 1966 MT				87	9	2
Oldemeyer et al. 1971 WY				61	17	22
\bar{x}	56	23	21	64	15	21

grasses (56%) in summer but used forbs (23%) and shrubs (21%) more equally. Sheep also exhibited a seasonal change to grasses (65%) in winter.

Nine studies of goats and 11 studies of sheep contained analyses of forage species used. Although many plant species were used, most were consumed at very low levels (<1% of diet; Laundré 1990). Data were summarized for only those 12 genera that occurred $\geq 1\%$ within the diet of at least sheep or goats (Table 2). The main genera used by goats and sheep in the summer were sedges (*Carex* sp.), wheatgrass (*Agropyron* sp.), bluegrass (*Poa* sp.), fescue (*Festuca* sp.), and bluebells (*Mertensia* sp.). Winter diets consisted mainly of sedges, wheatgrass, sagebrush (*Artemisia* sp.), and fescue.

Three studies (Pallister 1974, Stewart 1975, Dailey et al. 1984) presented data of food habits from sympatric populations of nonnative goats and native sheep. Pallister (1974) and Stewart (1975) primarily studied sheep but also recorded food habits of naturalized mountain goats in their study areas. The goats were descendants of releases made in the 1940s. Pallister (1974) found that summer diets of mountain goats consisted of 40% grasses and 60% forbs. During the same time sheep consumed 12% grasses, 55% forbs, and 32% shrubs. Although both species relied on forbs to a similar level, comparisons of forb species eaten indicated little overlap except clover (*Trifolium parryi*) (Pallister 1974: 48). Stewart (1975) found a similar reliance on grasses by sheep (44%) and goats (47%), but

TABLE 2. Comparison of percent use of preferred plant genera for goats and sheep. The percents are averages of the values reported in the literature.^a Sample size (*n*) is the number of reported values used to calculate the means.

Species	Summer		Winter	
	Sheep (<i>n</i> = 7)	Goats (<i>n</i> = 7)	Sheep (<i>n</i> = 10)	Goats (<i>n</i> = 5)
<i>Agropyron</i> sp.	6	9	15	4
<i>Carex</i> sp.	15	10	15	8
<i>Deschampsia</i> sp.	2	<1	<1	<1
<i>Festuca</i> sp.	8	5	12	18
<i>Poa</i> sp.	15	14	1	4
<i>Koeleria</i> sp.	<1	5	3	1
<i>Stipa</i> sp.	<1	<1	2	<1
<i>Artemisia</i> sp.	<1	<1	10	3
<i>Mertensia</i> sp.	2	6	0	<1
<i>Potentilla</i> sp.	4	1	<1	<1
<i>Salix</i> sp.	5	4	1	1
<i>Trifolium</i> sp.	5	2	0	<1

^aMills 1937, Hibbs 1967, Oldemeyer et al. 1971, Constan 1972, Peck 1972, Pallister 1974, Frisina 1974, Stewart 1975, Johnson et al. 1978, Johnson 1983, Johnson and Smith 1980, M. J. Thompson 1981, Adams and Bailey 1983, Campbell and Johnson 1983, Whitfield 1983, Kasworm et al. 1984, Keating et al. 1985, Martin 1985

goats relied most on *Poa* sp. while sheep were more evenly divided among three species: *Agropyron*, *Carex*, and *Poa* (Stewart 1975: 68, 98). Overall forb use by sheep and goats was also similar, 47% for sheep, 53% for goats, but specific use of forbs differed. Sheep relied on a variety of forb species while goat diets consisted mostly of *Arnica latifolia* and *Erigeron* sp. Dailey et al. (1984) conducted parallel feeding trials with captive goats and sheep on unoccupied range in Colorado. Their work indicated goats ate more forbs in summer (goats 88%, sheep 70%) and winter (goats 59%, sheep 22%), while sheep consumed more grasses (summer, 30% vs. 11%; winter, 75% vs. 27%).

For summer diets expressed in forage classes, overlap indices were high for separate (0.98) and comparative studies (0.93) (Fig. 1a). Resource overlap in winter, based on data from separate studies, was also high (0.99). For the comparative study from Colorado (Dailey et al. 1984), the winter overlap index was 0.64 (Fig 1a). For the pooled separate studies where forage species were identified, summer (0.86) and winter (0.80) indices were slightly lower than those for general forage classes (Fig. 1a). Summer overlap indices (Fig. 1a) for the two comparative studies in Montana (Pallister 1974, Stewart 1975), however, were substantially lower (0.32 and 0.55) than those for general forage classes (Fig. 1a). There were insufficient data to determine whether indices from the comparative studies differed statistically from the general diet index.

General Habitat Use

Oldemeyer et al. (1971) divided habitat used by sheep in Yellowstone National Park into three general types: forest, grass, and shrub. In winter they found that sheep used forest 13%, grass 78%, and shrub 9% of the time. When they divided the area based on terrain, they found sheep used "steep" areas 39%, rocky outcrops 14%, ridgetops 36%, hilly areas 8%, and level areas 4% of the time. Of the numerous structural/vegetational formations defined by Martin (1985) in Montana, sheep spent most of their summertime in the "alpine turf" formation (approximately 50%) and the "sparsely vegetated dirt scree" formation (approximately 28%). In spring, Frisina (1974) found sheep 36% of the time in "rocky reef" and 59% in "bunchgrass" types. Sheep use of the rocky reef type in fall increased to 64% and decreased to 34% in the bunchgrass type. Tilton and Willard (1982) divided their Montana study area into rockland, shrub/grass, open forest, and closed forest habitat types. They found sheep spending 14% of their time in the rockland type, 46% in the shrub/grass, 40% in the open forest, and 1% in the closed forest types.

Peck (1972) divided goat habitat in Montana into four types: timber, sliderock, ledge, and ridge. He found goats spending 4% of their summertime in timber, 36% in sliderock, 54% in ledge, and 6% in ridge areas. In winter, goats were seen 16% of the time in timber, 70% in ledge areas, and 14% of the time on ridges. M. J. Thompson (1981) found goats in

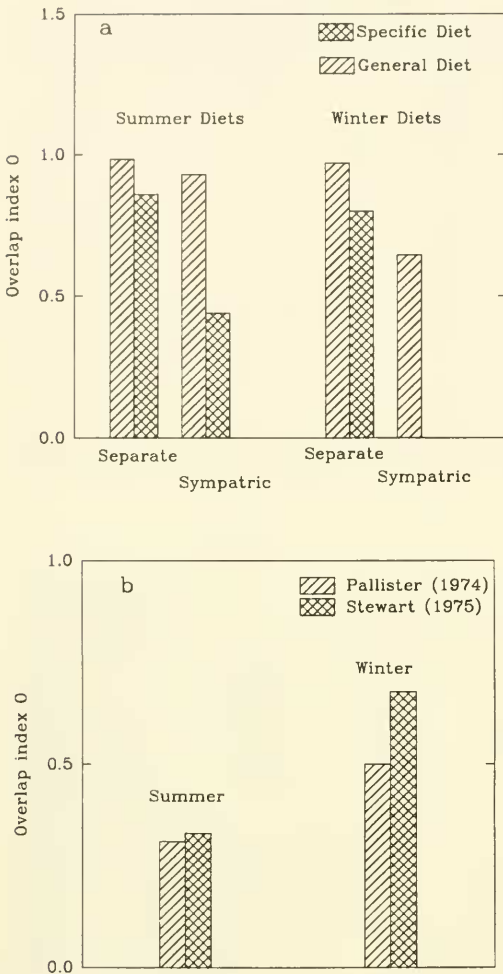


Fig. 1. Niche overlap indices for food habits (a) and habitat selection (b). Overlap indices for food are for pooled data from separate studies and data from comparative studies and are based on either general (grass, forbs, shrubs) or specific (to genera) food classifications. The index for sympatric specific summer diets is the mean of indices calculated from Pallister (1974) and Stewart (1974). The index for sympatric general summer diets is the mean from Dailey et al. (1984), Pallister (1974), and Stewart (1974). Indices for habitat selection are all from two comparative studies of sympatric sheep and goat populations.

Montana spending 90% of their summertime and 68% of their early wintertime on glacial cirques. In winter in the Bitterroot Mountains, Smith (1976) found goats 62% of the time in the "bunchgrass" association. Goats in Colorado spent 85% of their time in the substrate type described as "intermittent boulder"

by R. W. Thompson (1981). Adams and Bailey (1980) classified the habitat into alpine and subalpine areas. Within the alpine community they identified tundra and rock subcomponents. Goats spent 58% of their time during winter in the tundra and 42% in rock areas. The subalpine community was subdivided into rock, shrubs, and trees. Goats were seen 35% of the time in rock areas, 10% in shrub, and 55% in tree areas. Von Elsner-Schack (1986) studied goats in Alberta and divided the study area into rock, gravel, and grass substrate types. In spring-summer, goats used the rock substrate 24%, the gravel substrate 26%, and the grass areas 50% of the time.

Few studies examined habitat use by sheep and goats simultaneously. Chadwick (1974) found some habitat segregation but did not quantify the differences. Geist (1971) found that goats in winter spent approximately 52% of their time in sheer cliff areas while sheep spent only 28% of their time in these areas. In the two Montana studies of bighorn sheep, Stewart (1975: 68, 96) and Pallister (1974: 28, 56) also recorded habitat use by goats in their study areas. Habitat use overlap indices based on Pallister's (1974) data were low for summer (0.31) and winter (0.50). The summer overlap index (0.33) from Stewart's (1975) data was similar to Pallister's value, but the winter index (0.68) was slightly higher (Fig. 1b).

Another area of potential overlap between goats and sheep is the physical characteristics of the environment. Several investigators separately quantified habitat use by goats and sheep relative to distance from escape terrain, slope, and elevation (Table 3). The average distance to escape cover in summer was significantly greater for goats ($t = 6.04$, $n = 9$, $P < .01$). Average slope used did not differ within species between winter and summer but did differ significantly between species in both seasons ($F = 15.2$, $n_1 = 7$, $n_2 = 6$, $P < .01$), with goats using steeper areas (Table 3). No difference in use was found between species or seasons for average elevation. Thus, goats preferred steeper slopes and were found further from escape terrain than were sheep.

DISCUSSION

Wildlife biologists have been implicitly using data compiled separately on resource use of goats and sheep to formulate views

TABLE 3. Means (\pm SE, *n*) of physical habitat characteristics by sheep and goats. Distance to escape habitat (DEH) values are the maximum distances at which $\geq 80\%$ of the animals were found. Values for slope and elevation are the means of data reported in the literature. An asterisk next to a measurement indicates significant ($P < .05$) differences between sheep and goats. Footnotes list references of original data.

	Summer		Winter	
	Sheep	Goats	Sheep	Goats
DEH ^a	120 \pm 11.6 m, 4	305 \pm 25.6 m, 5*	278 \pm 103 m, 4	
Slope ^b	22 \pm 2.6°, 4	41 \pm 5.2°, 4*	24 \pm 6.5°, 2	47 \pm 8.4°, 3*
Elevation ^c	2655 \pm 325.3 m, 4	2799 \pm 320.8 m, 4	2431 \pm 306.5 m, 4	2354 \pm 376.7 m, 3

^aHjeljord 1971, Oldemeyer et al. 1971, Frisina 1974, Pallister 1974, McFetridge 1977, R. W. Thompson 1981, Tilton and Willard 1982, Fox 1983, Whitfield 1983, Martin 1985, Smith 1986
^bKuck 1973, Frisina 1974, Pallister 1974, Chadwick 1977, Smith 1976, R. W. Thompson 1981, Whitfield 1983, Martin 1985, Hayden 1989
^cFrisina 1974, Pallister 1974, Smith 1976, Adams and Bailey 1980, M. J. Thompson 1981, R. W. Thompson 1981, Whitfield 1983, Martin 1985, Hayden 1989

concerning competition between the two species. Differences found in this review between results from separate and comparative studies indicate a danger in using data from separate studies. Food habits data from separate studies, based on general forage classes and forage species, indicated extensive overlap in goat and sheep diets. Data on habitat use from such studies also indicated goats and sheep mutually used “grass” and “tree” habitat types and similar elevations in the subalpine/alpine zones. These data strengthen the commonly held consensus of extensive resource overlap and support concerns that goats and sheep might not coexist if resources are limiting. In contrast, data from comparative studies, where specific diet composition and habitat use are considered, indicate substantial reductions in overlap when goats and sheep co-occur in an area.

Consequently, comparisons of data from separate studies might be useful in determining the amount of resource overlap that is possible between similar species but cannot be used to estimate what that overlap would be in sympatry. Only results from comparative studies of sympatric populations can be used to predict how two species will interact. Even in such comparative studies, my analysis indicates that researchers should avoid the use of general resource categories.

Currently, we have only two comparative studies of detailed resource use by goats and sheep. This is hardly a sufficient data base from which to draw valid conclusions concerning resource overlap or the potential for competition between goats and sheep. If scientifically sound conclusions about interactions between goats and sheep are to be formulated, additional comparative studies are

needed. Only after such studies can we address questions concerning competition and competitive interactions between sheep and goats.

If the pattern of reduced resource overlap in sympatry withstands further study, it may be the result of resource partitioning. Whether this is the case and whether this resource partitioning is in turn a result of competitive interactions cannot be addressed with this data base. If resource partitioning is found to be a major factor in the coexistence of sympatric native goat and sheep populations, the low resource overlap found in the two comparative studies involving nonnative goats indicates goats and sheep may also exhibit such partitioning when one or the other species is an exotic introduction. However, Adams et al. (1982) cautioned that certain conditions (land development, agricultural activity, etc.) might limit selection options for one or the other species. In such cases resource partitioning may not be possible, resulting in extensive overlap of resource use between goats and sheep, possibly to the detriment of one of the species if resources are limiting.

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